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Species turnover drives functional turnover with balanced functional richness in a Patagonian demersal assemblage.

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Abstract

Marine communities are changing at an accelerated rate because of anthropogenic stressors such as global warming and overfishing. Community compositional change over time (temporal β diversity) is mainly driven by the replacement of species. The consequence of this change on community functioning is still unclear. In this study, we assessed the magnitude and direction of both taxonomic and functional compositional change in a demersal community subject to fishing and incipient sea warming over a recent 12-year period. We also evaluated the relative roles of turnover and nestedness components on both dimensions of temporal β diversity and identified which species are driving compositional change. Compositional data was collected during five surveys that took place between 2006 and 2018. We used linear mixed models to test for temporal change in species richness and taxonomic and functional dissimilarity and its components. While species richness remained constant, taxonomic and functional dissimilarity increased through time, with turnover contributing most to total dissimilarity in both cases. Taxonomic turnover of around 15% of species per decade produced a functional replacement of 13% per decade. The main functional change is probably due to the spatial expansion of three species of crustaceans which are bringing functional novelty to certain areas of the gulf. We found that local extinctions and colonization were balanced, which suggests that species richness is being regulated at the local scale within the gulf. We also found a balance in functional richness, which leads us to infer that this variable is also being regulated at the community level.

Key words: β diversity, functional traits, global change, marine fish, marine crustaceans, trawl fishing**.**

1. Introduction

The Anthropocene is experiencing accelerated shifts in biodiversity across the globe as a consequence of human-related pressures that result in biodiversity loss, and changes in occupancy (local extinctions and colonizations) and in the relative abundance of persistent species (D'Agata et al. 2014, Newbold et al. 2019, Dornelas et al. 2019, Storch et al. 2022). There is, however, evidence that conclusions on biodiversity trends are dependent on the nature of the data being drawn on. Assemblage-level approaches have found that local extinction and colonization rates are both accelerating, but at similar rates (i.e., they are balanced), reflecting an accelerated replacement of species and constant taxonomic richness. Community compositional change in local assemblages over time -temporal β diversity- worldwide is thus driven by shifts in the identity rather than the number of species that constitute them (Dornelas et al. 2014, Magurran et al. 2015, Dornelas et al. 2019, Blowes et al. 2019). The consequence of this change in species composition for community functioning and resilience is still unclear (Pandolfi & Lovelock 2014, Magurran et al. 2019, Mori et al. 2018).

Temporal β diversity (Dornelas et al. 2014) is driven by two distinct processes, turnover (i.e., species replacement) and nestedness (i.e., a type of richness difference pattern characterized by the species at a site being a strict subset of the species at a richer site; Baselga 2010, Baselga & Orme 2012, Legendre 2014). Since species play different roles in the communities that they are part of, shifts in taxonomic composition may have varying consequences for the community's functional diversity (Meynard et al. 2011, McGill et al. 2015), such as the replacement or gain/loss of functional traits. If all species are functionally unique, species and trait composition should change at a similar rate. Conversely, the addition or replacement of a new species may not be reflected in functional diversity if the combination of the functional traits it brings is redundant within the original community (Villéger et al. 2013, Bevilacqua & Terlizzi 2020). Species that play similar roles in a community (i.e., are functionally redundant) have a similar position in the functional niche, which is represented by a multidimensional space where the axes are associated with different traits (Rosenfeld 2002). On the other hand, species that are significantly different from the rest of the community in terms of traits are referred to as functionally distinct species (Violle et al. 2017). If these species are lost and no other species can fill the void of the potentially lost function, it can have a significant effect on ecosystem functioning (Mouillot et al. 2013, Violle et al. 2017).

The computation of the volume of the functional space occupied by a community allows for the measurement of functional β diversity indices and its decomposition into its components in a similar way to that proposed by Baselga & Orme (2012) for taxonomic β diversity (Villéger et al. 2011, 2013). This allows for a direct comparison of the two dimensions of β diversity (Villéger et al. 2013). Additionally, the computation of the functional distinctiveness index (Murgier et al. 2021) allows for the quantification of the functional dissimilarity of a

given species compared to all other species in the regional pool. Evaluating the level of congruence of taxonomic and functional temporal change can shed light on the ecological processes underlying the functioning of biological communities (Jarzyna & Jetz 2017, White et al. 2018, García-Navas et al. 2022) and underpinning ecosystem resilience (Tilman et al. 2006).

Across different habitats and groups of organisms, taxonomic compositional change during the Anthropocene is dominated by species turnover within assemblages (Blowes et al. 2019, Dornelas et al. 2019). Marine assemblages are showing some of the highest rates of species turnover, at around 10-28% of species per decade (Dornelas et al. 2014, Blowes et al. 2019). This global pattern is largely driven by the rapid behavioral response of marine species (mainly fish) to ocean warming and the few geographic barriers in marine systems that allow them to shift their geographic range following their thermal limits (Sunday et al. 2012, Blowes et al. 2019, Pinsky et al. 2019). Another global driver behind this pattern is fishing, which, coupled with global warming, seems to be the main driver of high taxonomic turnover in demersal assemblages (Ellingsen et al. 2015; Magurran et al. 2015; Gotelli et al. 2021). Additionally, recent studies from catch data show that different demersal assemblages around the world are changing their functional diversity as a consequence of the joint effects of fisheries and sea warming (Gianelli et al. 2019, Trindade-Santos et al. 2020, Rincón-Díaz et al. 2021, Perez & Sant'Ana 2022). Among the main changes reported, there has been a shift in the composition of catches from fishes to crustaceans, which suggests changes in the structure and functioning of these communities (Anderson et al. 2011, Boenish et al. 2022). However, the patterns of change in terms of functional temporal β diversity of demersal assemblages have not been assessed so far.

The Patagonian Shelf Large Marine Ecosystem south of 40° S is one of the biogeographic regions of the world where the effects of global change on marine fish diversity have been least studied (Rincón-Díaz et al. 2021, Galván et al. 2022). For this region it was estimated a positive trend in sea surface temperature of 0.04 °C per year north of 50° S for the period 2002-2020 (Saraceno et al. 2022). Related to this incipient warming and coupled with the effects of fisheries, a research-based assessment suggests that coastal fish assemblages in Patagonia may be undergoing high compositional change (Galván et al. 2022). However, the magnitude and direction of this compositional change have not been evaluated yet.

Here, we assess the magnitude and direction of change in both taxonomic and functional temporal β diversity of a Patagonian demersal assemblage that has been subjected to intense fishing trawling since 1971 and that could be experiencing sea warming. We hypothesize that the rate of change in species composition is within the order of magnitude of that of other marine assemblages around the world that are experiencing accelerated species replacement during the Anthropocene, and that this taxonomic change is leading to a change in the functional composition of the assemblage.

To do this we used survey data to (1) quantify temporal change in species richness and both taxonomic and functional composition of a demersal community over a recent 12-year period;

(2) examine the relative roles of turnover and nestedness components on both dimensions of temporal β diversity; and (3) identify the main species that may be responsible for functional change as a consequence of their spatial expansion or retraction within the study area.

2. Methodology

2.1 Study area and the demersal assemblage assessment

We conducted this study in the San Matías Gulf (SMG), which is a semi-closed basin located in northern Patagonia, Argentina, and covers approximately 20000 km^2 (Gagliardini & Rivas 2004) (Fig. 1). During austral spring and summer (from October until March), a tidal front divides the gulf in a SW-NE direction, differentiating two water masses. The northwestern mass is characterized by higher temperatures and salinity, lower concentrations of nitrate and chlorophyll *a* (chl *a*), and a low water exchange rate. The southeastern mass, on the other hand, has lower temperatures and salinity and higher concentrations of nitrate and chl *a*, and is strongly influenced by the inflow of colder waters from the south (Piola & Scasso 1988). The front vanishes in the colder months (Gagliardini & Rivas 2004, Williams et al. 2010).

From a biological standpoint, the SMG is in a transition zone between two biogeographic regions, and so many species native to each of these regions share this common habitat (Balech & Ehrlich 2008). Others, such as the Argentine hake *Merluccius hubbsi*, go through their entire life cycle within the gulf basin (Di Giacomo et al. 1993, Sardella & Timi 2004, González et al. 2007, Ocampo Reinaldo et al. 2013). The demersal community has been subjected to bottom trawling since 1971 (González et al. 2004, Romero et al. 2008, Ocampo Reinaldo et al. 2016), with the Argentine hake as the historical main target (González et al. 2007, Romero et al. 2008, 2013, Ocampo Reinaldo et al. 2013, 2016). However, changes in landing composition over the years suggest shifts in community structure (Romero et al. 2008, 2013). Since 2012 these changes seem to have accentuated, with an increase in the abundance of crustaceans such as the squat lobster *Munida gregaria* (Alonso et al. 2019) and the Argentine red shrimp *Pleoticus muelleri*, the latter leading to the development of a new fishery (Narvarte et al. 2013). Since these changes could be a sign of compositional change towards a community with a greater representation of crustaceans, in this study, we considered the entire demersal assemblage, including both fish and macroinvertebrates.
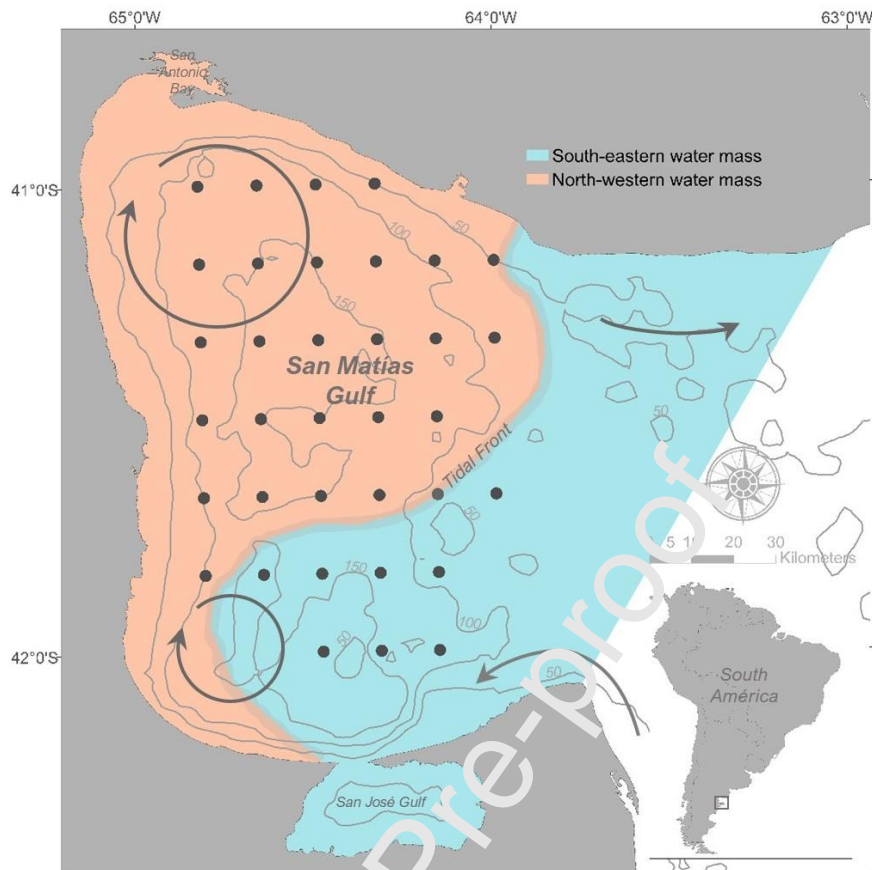
Figure 1. Study area showing a schematic drawing of the main frontal system when it is fully formed in summer (gray shadow) and the mean flow of the San Matías Gulf (gray arrows) (based on Piola & Scasso 1988, Acha et al. 2004, Tonini et al. 2013). The black dots represent the 35 hauls sampled each year and taken into consideration for the construction of incidence matrices.

2.2 Data sources

Data on the composition of the demersal community were collected during five surveys that took place in the spring of 2006, 2007, 2009, 2016 and 2018. These surveys followed a regular grid of 35 hauls with demersal trawling gear and they were carried out at depths between 30 and 160 meters (Fig. 1; Ocampo Reinaldo 2010). Trawl hauls were conducted with an average duration of 30 minutes at a speed of 3 knots and covered a mean swept area of 0.06 km2 per haul. For each haul, a sample of six fish boxes was taken and the individuals collected in the sample were identified to species level; a few species of the same genus were aggregated when identification to species level wasn't possible. The assemblage assessed in the present study included all species of fish and macroinvertebrates with demersal habits and excluded species with exclusively benthic habits (sessile species and those that do not have significant vertical migrations; Table S1).

In order to analyze the community's functional composition and its temporal change, we first characterized the pool of species using a set of 11 ecologically relevant functional traits (Table S2; Trinidade-Santos et al. 2020). The chosen traits give information on the species life history (growth rate, ratio between consumption and biomass and trophic level), their

morphology (body shape and swimming mode), their reproductive strategy (generation time, length of first maturity and reproductive guild) and environmental conditions (position in the water column, maximum depth and mean temperature preference). For "trophic level" and "ratio between consumption and biomass" (Q/B) we used local values when available to understand the effect of the species on the trophic structure of this particular assemblage and location. We used data from an ECOPATH network model for the SMG's food web to inform these two traits, with "functional groups" representing all trophic levels of the "demersal-pelagic food web" (Ocampo Reinaldo et al. 2016). These groups were sometimes disaggregated to species level but often built by aggregating more than one similar species (from a trophic standpoint), depending on abundance, commercial/ecological value, and available information (Ocampo Reinaldo et al. 2016). For the remaining traits, we consider information that summarizes the general biological range of each species. This enables us to understand the global characteristics of the species, independent of local conditions. For example, a species with a high global mean temperature preference could potentially indicate greater resilience to temperature increases associated with climate change, regardless of specific local temperature records. Those values were collected from the databases FishBase (Froese & Pauly 2021) and SeaLifeBase (Palomares & Pauly 2021), and primary literature when information in the databases was insufficient.

Due to data limitations, we assumed that traits for each species did not change between 2006 and 2018 and that there is no intraspecific variability. The traits assigned to each of the species that make up a community were later represented as coordinates in a multidimensional space which was then used to describe the community's functional composition and to compute functional diversity indices (Villéger et al. 2008).

2.3 Data analysis

In order to test the temporal change in taxonomic composition, we calculated the dissimilarity with the baseline year (2006) for each sampled year using the Jaccard dissimilarity index (Baselga 2010). We assessed functional dissimilarity using the framework proposed by Villéger et al. (2011), which is based on the concept of functional space and the computation of the FRic index (Villéger et al. 2008, 2013). This index measures functional range and is influenced only by species identity, particularly those with extreme functional traits. Functional dissimilarity is defined as the percentage overlap between the convex hulls of each sample. We chose this dissimilarity index because it is based on Baselga (2012)'s taxonomic β diversity index and its partitioning methodology, facilitating the comparison of both dimensions of temporal β diversity. This index is also useful for identifying the effect of disturbances such as overfishing and ocean warming (Legras et al. 2018), since these two scenarios affect species with extreme trait values (eg. fish with higher body size as shown in Mouillot et al. 2013).

We explored the relative roles of turnover and nestedness to both taxonomic and functional dissimilarity, following the methodology proposed by Baselga & Orme (2012) and Villéger et al. (2013). Dissimilarity indices range between zero and one. The Jaccard dissimilarity index

for taxonomic β diversity (Jac) equals zero when two years have the same pool of species and reaches one when two years have a totally dissimilar pool of species. Taxonomic turnover, which measures the simultaneous species gain and loss between two years (Legendre 2014), equals zero when all species occurrences are the same in both years, and it equals one when there are no shared species (Baselga 2010). Taxonomic nestedness, on the other hand, equals zero when both years have the same number of species and it tends to one when one year hosts a small subset of the species from the other year (Baselga 2010). For functional dissimilarity, functional turnover reaches one when the convex hulls of the two time points being compared have the same volume and don't overlap at all in the functional space (Villéger et al. 2013). Functional nestedness, on the other hand, tends to its maximum (one) when one community hosts a subset of the species present in the other and there is a reduction/increase in the volume of the functional space (Villéger et al. 2013).

Functional space for the SMG's community was calculated using each haul's community incidence matrix for each year, and a functional coordinates matrix derived from a principal coordinates analysis (PCoA) based on Gower's distance. The use of Gower's distance allowed for the inclusion of both continuous and categorical traits (Villéger et al. 2008). Ordination methods such as a PCoA also avoid possible correlations that can come with the selection of too many traits for one function (Legras et al. 2020). We limited the number of dimensions of the functional space so that they explained over 50% of the variation, which resulted in the selection of the first three PCoA axes.

We employed linear mixed models to analyze biodiversity trends and test for temporal changes in species richness, as well as taxonomic and functional composition. Overall slopes for species richness and β diversity indices were estimated by allowing each haul to have a different intercept but constraining all of them to have the same slope (Dornelas et al. 2014). It should be noted that our goal was not to study spatial differences within the gulf (i.e. between haul locations), but rather to determine if there is a significant local average trend that may explain inter-annual changes across the entire gulf (i.e. accounting for spatial variability). For β diversity indices, the regression slopes are a measure of the rate of change in species/trait composition. Steep positive slopes represent divergence in composition from the baseline year, whereas negative slopes indicate that earlier samples were more dissimilar from the baseline than later samples. Slopes (positive or negative) that are close to zero represent little or no long-term change in species or trait composition (Dornelas et al. 2014).

Regarding model diagnostics, visual inspection of residual plots did not reveal any obvious deviations from normality, except for nestedness data that was slightly skewed (Fig. S1). However, we did not transform the data since linear mixed effect models are robust to violations of the normality assumption and data transformation would impact model interpretability (Schielzeth et al. 2020). All analyzed variables meet the assumption of homogeneity of variances as assessed by Levene's test (p>0.05; Table S3).

Lastly, we identified the main species that may be driving functional change as a consequence of their spatial expansion or retraction within the study area. Taking advantage of the regular

spatial design of the surveys, we used each species' frequency of occurrence in the hauls (i.e., the number of hauls in which each species was present divided by the total number of hauls conducted per year) as an indicator of their occupancy in each year. A species is considered to have maximum occupancy (one) if it appears in all hauls of a survey, and zero occupancy if it is absent in all hauls. We split the time series into two distinct periods (2006-2009 and 2016-2018) and focused on occupancy changes between them. The change in occupancy was calculated as the difference in a species' occupancy between the later period and the earlier one. Changes in occupancy ranged from −1 to 1, with a value of −1 indicating a species was present in all hauls in the early period but absent from all hauls in the late period, and a value of 1 indicating the opposite.

Next, we assessed whether species that are changing their occupancy could also be driving functional change. We focused on vertex species of the global functional space, as the dissimilarity indices used in this study highlight changes in these species. These are the species we can confidently predict will be vertices in any haul when present, and their changes in occupancy will influence the functional dissimilarity indices. However, it's worth noting that some species that are not vertices in the global functional space could potentially become vertices in some hauls and thus also affect the dissimilarity indices. We also calculated each species' functional distinctiveness (Murgier et al. 2021) to account for the trait originality of these species, as a vertex position doesn't necessarily equate to functional rarity. We then assessed the relationship between functional distinctiveness, vertex species, and occupancy change. Following Murgier et al. 2021, we concentrated on functionally common and functionally distinct species by selecting the first and last quartiles of distinctiveness, respectively. The first group (Q1) comprised the most functionally common species, while the fourth group (Q4) included the most functionally distinct ones.

All analyses were performed in R (R Core Team 2022). Mixed models were generated using the function *lmer* from the package lme4 (Bates et al. 2015). Taxonomic dissimilarity metrics were computed with the package betapart (Baselga & Orme 2012) and functional dissimilarity indices were calculated with the function *multidimFbetaD* developed by Villéger et al. (2013). Vertex species were identified using the *vertices* function from the mFD package in R (Magneville et al. 2022). Functional distinctiveness was computed with the function *distinctiveness* from the package funrar.

3. Results

At a regional level, the demersal assemblage of SMG hosted a total of 53 species during the study period (Table S4), out of which 48 were fishes (including species of the Actinopterygii, Elasmobranchii and Holocephali subclasses) and five were macroinvertebrates (including species of the Crustacea subphylum and Cephalopoda class). The richness observed in each haul ranged from 6 to 26 species. Estimated taxonomic richness did not change significantly throughout the study period (Fig. 2, Table 1), with a mean value of 14 (± 2) species per haul for all years sampled (local richness) (Table 2).

For β diversity, the overall slope for both taxonomic and functional Jaccard dissimilarity was positive and significantly different from zero (Fig. 3, Table 1), with estimated taxonomic total dissimilarity (Jac) with the baseline year (2006) rising from 0.46 in 2007 to 0.63 in 2018 and estimated functional total dissimilarity (FJac) increasing from 0.42 in 2007 to 0.57 in 2018 (Table 2). We also found an increase in both taxonomic and functional turnover through time (from 0.37 to 0.54 and from 0.20 to 0.34, respectively; Table 2). Nestedness, on the other hand, did not change in any case (with a constant mean value of 0.10 for taxonomic nestedness, and functional nestedness going from 0.22 to 0.24) (Table 1; Fig. 3). Taxonomic turnover consistently accounted for most of species total dissimilarity (around 80%; Table 2), whereas functional turnover had a lower contribution than nestedness at first, and then increased to become the main component of dissimilarity (from less than 50% to around 60% of total dissimilarity; Table 2).

Table 1. Linear mixed models fit by maximum likelihood to predict each β diversity index with the sampled year. The models included the hauls as a random effect. Conditional (cond.) R^2 refers to the model's total explanatory power, and marginal (mar.) R^2 refers to the fixed effects alone. Confidence Intervals (CIs) and p-values were computed using a Wald t-distribution approximation.

| *Index* ~ Year	Cond. R^2	mar. R^2	Slope	95% CI	p
Species richness	0.38	0.0019	0.034	[-0.058, 0.126]	0.468
Taxonomic dissimilarity	0.51	0.29	0.015	[0.012, 0.019]	<0.001
Taxonomic turnover	0.29	0.1	0.015	[0.011, 0.02]	<0.001
Taxonomic nestedness	0.11	0.00003	-0.0001	[-0.002, 0.002]	0.939
Functional dissimilarity	0.65	0.4	0.014	[0.01, 0.018]	<0.001
Functional turnover	0.22	0.11	0.013	[0.007, 0.019]	<0.001
Functional nestedness	0.26	0.001	0.001	[-0.005, 0.007]	0. 894
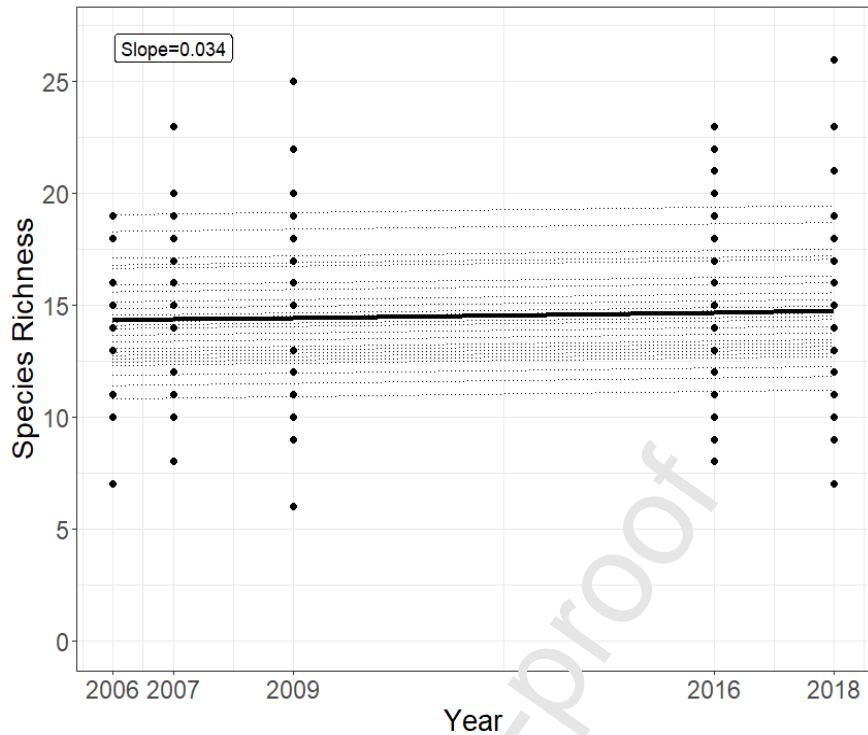
Figure 2. Linear mixed model for alpha diversity, measured as the number of species present in each year sampled. The solid line corresponds to the mean slope of the fitted mixed model, in which a single slope, but different intercepts were fitted to all hauls, dashed lines correspond to the regressions fitted for each haul. The dots represent each haul.

Table 2. Alpha diversity and taxonomic and functional temporal β diversity (and its components) predicted by mixed linear effects models and the contribution of turnover and nestedness (% inside brackets) to total dissimilarity for every year. In square brackets the standard deviation.

|		2006	2007	2009	2016	2018
Taxonomic alpha diversity		14.34 [± 0.51]	14.38 [± 0.49]	14.45 [± 0.46]	14.68 [± 0.51]	14.75 [± 0.55]
Taxonomic β diversity	Total dissimilarity	0 (baseline year)	0.46 [± 0.016]	0.49 [± 0.015]	0.60 [± 0.015]	0.63 [± 0.016]
	Turnover	0	0.37 [± 0.019] (79%)	0.40 [± 0.016] (80.4%)	0.51 [± 0.016] (84%)	0.54 [± 0.019] (84.8%)
	Nestedness	0	0.10 [± 0.011] (21%)	0.10 [± 0.008] (19.6%)	0.10 [± 0.008] (16%)	0.10 [± 0.01] (15.2%)
Functional β diversity	Total dissimilarity	0	0.42 [± 0.03]	0.45 [± 0.02]	0.55 [± 0.02]	0.57 [± 0.03]
	Turnover	0	0.20 [± 0.024] (47.6%)	0.22 [± 0.02] (48.88%)	0.31 [± 0.02] (56.4%)	0.34 [± 0.024] (59.6%)
	Nestedness	0	0.22 [±0.026] (52.4%)	0.23 [±0.023] (51.12%)	0.23 [±0.023] (43.6%)	0.24 [±0.026] (40.4%)
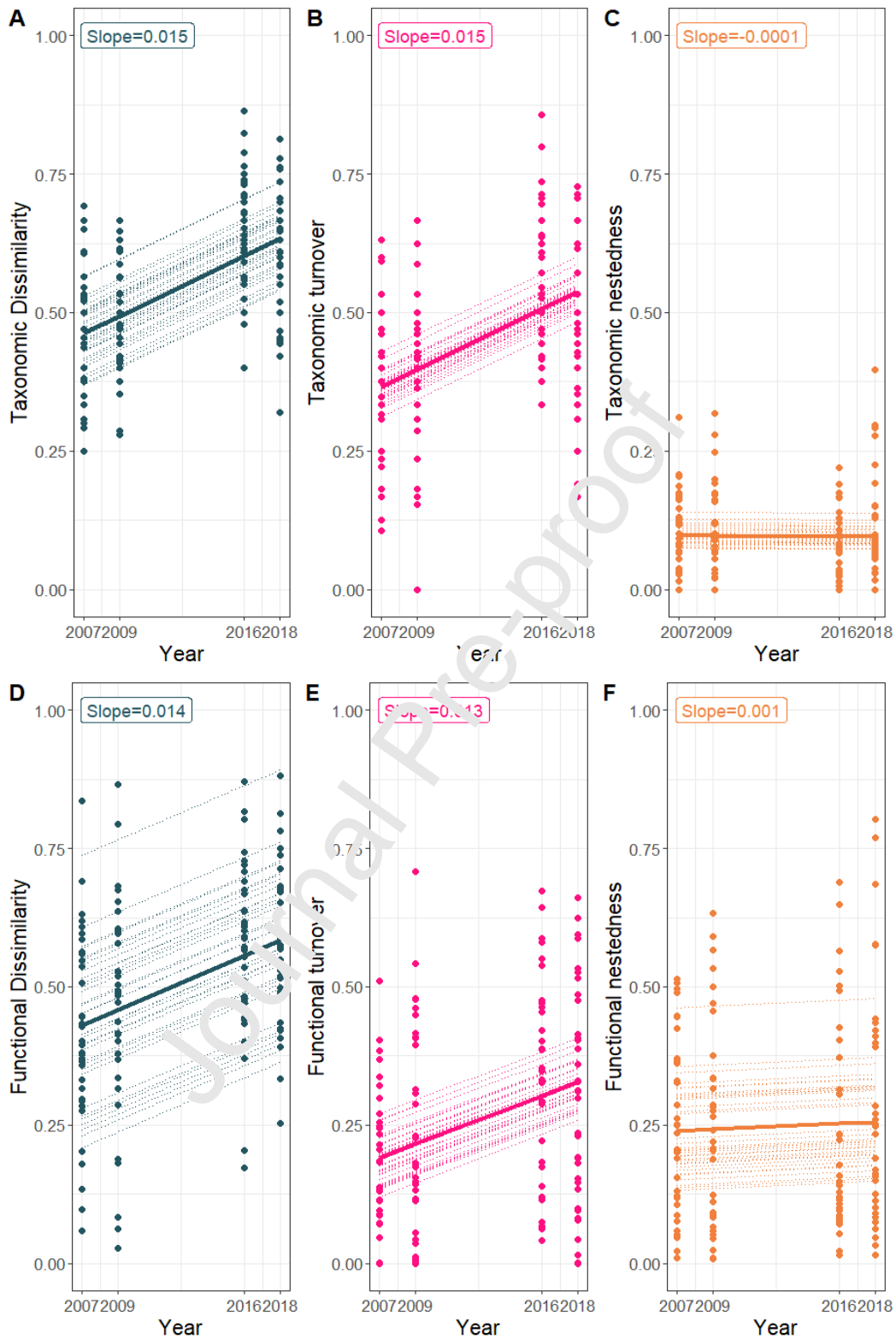
Figure 3. Linear mixed models for temporal β diversity. β diversity (blue), measured as the Jaccard dissimilarity index between each sampled year and the baseline year (2006), was partitioned into its turnover (pink) and nestedness (orange) components for both the taxonomic (A, B, C) and functional (D, E, F) facets of diversity. The solid lines correspond to the mean slope of the fitted mixed model, in which a single slope, but different intercepts were fitted to all hauls, dashed lines correspond to the regressions fitted for each haul. Turnover consistently accounted for a higher fraction of the observed dissimilarity (dots) in both metrics.

Among the 53 species that constitute the demersal assemblage, we observed varying trends in occupancy between the two time periods (2006-2009 and 2016-2018). Specifically, 24 species experienced a decrease in occupancy, 27 species saw an increase, and occupancy remained constant for two species (Fig. 4, Fig. S2). The average rate of change in occupancy between these two periods was 0.12, signifying a shift in occurrence across approximately nine hauls.

Regarding the position of species within the functional space of the community, we identified 19 vertex species (triangles in Fig. 4). Of these, 8 are increasing in occupancy (green triangles) , 9 are decreasing (red triangles), and 2 have remained constant (blue triangles). Among the 8 vertex species increasing in occupancy, 7 are functionally distinct (Q4), including the silvery lightfish *Maurolicus stehmanni*, the blue shark *Prionace glauca*, the Argentine red shrimp *Pleoticus muelleri*, the squat lobster *Munida gregaria*, the mantis shrimp *Pterygosquilla armata*, the spotback skate *Atlantoraja castelnaui*, and the yellownose skate *Dipturus chilensis*. The remaining vertex species increasing in occupancy, the Parona leatherjacket *Parona signata*, has intermediate distinctiveness values. Of the 9 vertex species decreasing in occupancy, 3 are functionally distinct (the Argentine goatfish *Mullus argentinae*, the ray *Bathyraja* sp., and bignose fanskate *Sympterygia acuta*) and 3 are functionally common (the cochero *Dules auriga*, the silver warehou *Seriolella porosa*, and picked dogfish *Squalus acanthias*). The remaining 3 vertex species decreasing in occupancy (the freckled sand skate *Psammobatis lentiginosa*, the flounder *Xystreuris rasile* and the blotched sand skate *Psammobatis bergi*) have intermediate functional distinctiveness values. Finally, among the two species with constant occupancy between periods, one is functionally common (the tope shark *Galeorhinus galeus*) and one has intermediate distinctiveness values (the Argentine hake *Merluccius hubbsi*). Out of these 19 vertex species, only five had occupancy changes higher than the mean rate of change (0.12): the flounder *X. rasile*, the argentine red shrimp, the squat lobster, the mantis shrimp and the skate *D. chilensis*.
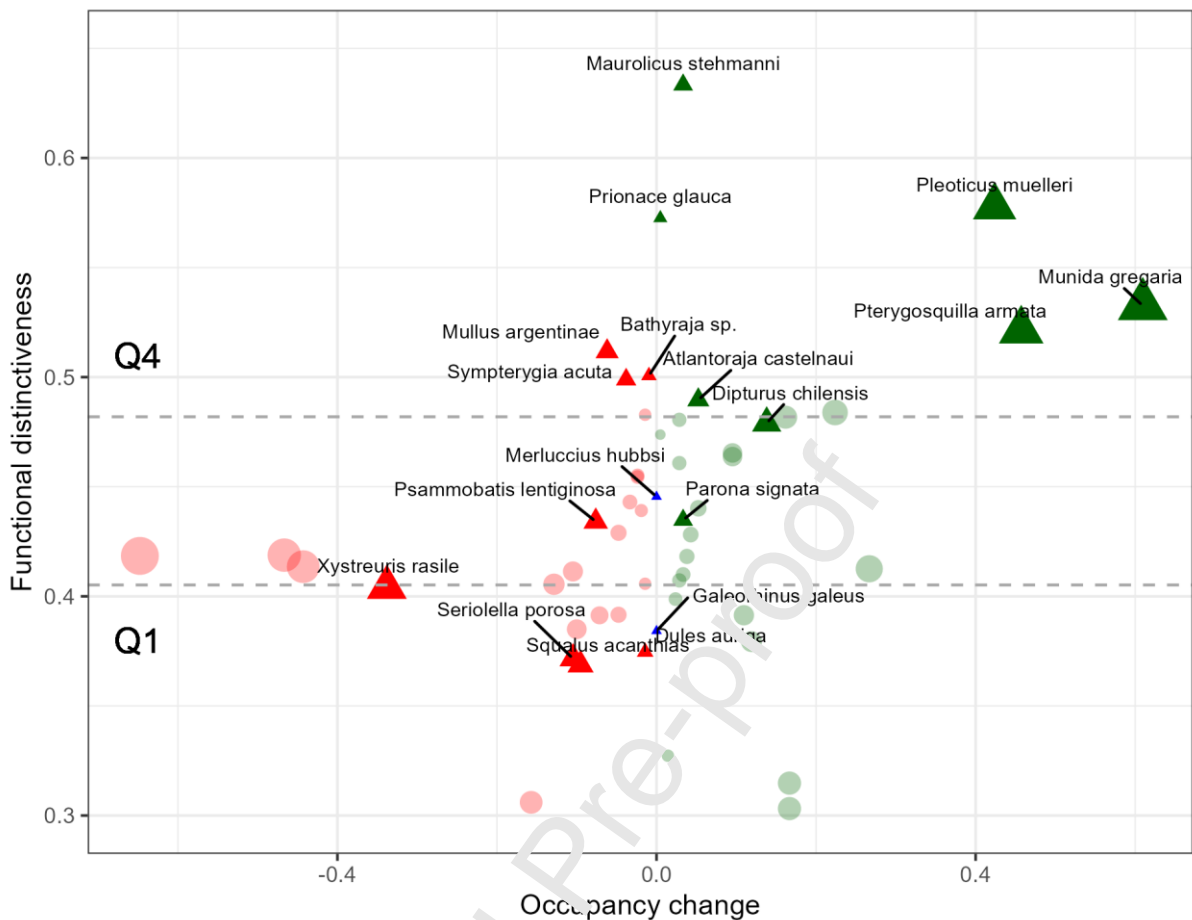
Figure 4. Relationship between species' occupancy change and functional distinctiveness. Triangles represent species that are vertices in the global functional space and the circles those that are intermediate species in the global functional space. Occupancy change direction is represented by colors. Red = decrease in occupancy, green= increase in occupancy, blue= occupancy remained constant. The horizontal dotted lines indicate the delineation of the two groups of functional distinctiveness (Q1 = Quartile 1, functionally common species; Q4 = Quartile 4, functionally distinct species). The size of the points is proportional to the magnitude of occupancy change.

4. Discussion

Our results show that the demersal community of the SMG is undergoing significant compositional change due to a substitution of taxa (taxonomic turnover) which is driving functional replacement through time (functional turnover) without significant changes in species richness. This aligns with recent studies that have shown that species richness is unrelated to temporal turnover over a range of marine ecosystems, with communities' composition shifting even when species richness remains constant (Dornelas et al. 2014, Magurran et al. 2015, Blowes et al. 2019). Our results provide further evidence that marine biodiversity change worldwide is dominated by substitution of taxa rather than net loss.

Here, for the first time within the Patagonian Shelf Large Marine Ecosystem, we evaluated temporal taxonomic and functional β diversity trends. We found that total taxonomic dissimilarity increased with a slope of 0.015 indicating a community composition change of 15% per decade. This magnitude of change is within the range of estimates for other marine

communities that are experiencing rapid reorganization, which show an increase in compositional change of approximately 10-28% species per decade (Dornelas et al. 2014, Blowes et al. 2019). A research-based assessment conducted in a larger maritime area of central Patagonian Shelf reported a higher number of newcomer species compared to the SMG, which suggest that the rate of change in both taxonomic and functional temporal β diversity could be even higher in that area than the rate reported in this study (Galván et al. 2022). Additionally, this study further corroborates the dominance of species replacement as the main driver of compositional change in both terrestrial and marine realms (Magurran et al. 2019). Our β partitioning revealed that the turnover component increased over time and accounted for almost all the total taxonomic dissimilarity (accounting for almost 85% of total dissimilarity by the end of the study period).

Given the different roles that species play within communities and that their substitution is rarely of like with like (Hobbs et al. 2006, Dornelas et al. 2014), we evaluated the congruence between taxonomic and functional β diversity trends. We found that an increase in species replacement resulted in a significant rise in functional dissimilarity (14% of functional change per decade). Specifically, functional turnover increased with a slope of 0.013 (i.e., change of 13% of the volume of functional space occupied per decade), while the nestedness component remained constant throughout the study period. The positive rate of functional turnover suggests an annual increase in the change of the position of the volume occupied by the demersal assemblage in the functional space compared to the first year sampled (2006). The constant functional nestedness implies that the volume within the functional space did not change. This indicates that the community's functional richness was stable despite changes in functional composition.

Recent studies show that regulation at the community level is a widely distributed phenomenon (Gotelli et al. 2017). This regulation was observed in species richness and total abundance (Gotelli et al. 2017; Dornelas et al. 2019). Moreover, any balance in a variable quantified for an entire community would be consistent with community-level regulation (Gotelli et al. 2017). Here we found a rise in taxonomic turnover and constant taxonomic nestedness, indicating a balance between "winners" and "losers" in terms of occupancy (Dornelas et al. 2019). This suggests that local extinctions are offset by an equivalent number of species colonizing new areas within the gulf. But going beyond, we also found a balance in functional richness, which leads us to infer that this variable may be also being regulated. In a recent study, Tsianou et al. (2021) examined the temporal beta diversity of a bird community and found high taxonomic dissimilarity but negligible functional dissimilarity. They proposed that this might be due to species with extreme trait values persisting over time and retaining in this way the volume of functional space. They suggest that the stability in functional diversity may imply ecosystem functioning is maintained despite changes in species composition. Like Tsianou et al. (2021) we found that the assemblage maintains the volume of functional space throughout the study period, but with a significant change in functional composition. Turnover dominates both aspects, with vertex species being replaced by other vertex species. This pattern suggests the ecosystem functioning is maintained but in a different place of the

functional space. Further studies in other communities and habitats are needed to know if this is a widespread pattern and to understand how the functional space of a community might be regulated in the face of different disturbances.

The observed functional change appears to be mainly associated with the increased occupancy of three crustacean species: the squat lobster *Munida gregaria*, the mantis shrimp *Pterygosquilla armata*, and the Argentine red shrimp *Pleoticus muelleri*. These species are functionally distinct within the community, introducing functional novelty to those hauls where they were initially absent. The expansion of the Argentine red shrimp within the SMG since 2012 (Narvarte et al. 2013) is seemingly connected to its increased presence since 2005 in the sector of the Patagonian shelf outside the gulf (de la Garza & Moriondo Danovaro 2020). The squat lobster's expansion, on the other hand, has been linked to reduced predator pressure due to overfishing (Diez et al. 2016). However, the exact causes of their rise within the SMG remain uncertain. Crustaceans in general exhibit traits that make them more resilient and enable them to adapt and benefit from anthropogenic pressures such as overfishing (Boenish et al. 2022). These traits include a lower trophic position, detritus-feeding ability, low temperature sensitivity, rapid growth, and effective parental care strategies (Vinuesa & Varisco 2007, Boenish et al. 2022). Our functional diversity analyses considered traits related to trophic level, growth, temperature preference, and reproductive guild, which reflect these advantageous characteristics. While our study did not directly evaluate this aspect, these resilience-enhancing traits common to crustaceans could be contributing to the observed rise in these species. Further research should explore this potential connection. On the other hand, the SMG is an ecotone of two biogeographic regions (Balech & Ehrlich 2008) and might be prone to colonization by functionally diverse species. In line with this, a previous network analysis of the SMG's food web suggests the ecosystem is still maturing, with more energy produced than consumed (Ocampo Reinaldo et al. 2016), making it susceptible to colonization by species that can be efficient (i.e. crustaceans) to occupy any available niches due to environmental changes or related to changes in the abundance of upper trophic levels (i.e., pathways release; Ocampo Reinaldo et al. 2016, Svendsen et al. 2020).

Methodological Considerations

The methodology employed in this study, which involves averaging across multiple hauls (samples) throughout the entire gulf, has both strengths and limitations. A key advantage is that a significant average slope across all hauls suggests a widespread species replacement throughout the gulf. However, this approach may mask local variations in species replacement. While an average slope provides a general overview, differences between hauls are not ruled out. Some hauls may exhibit more pronounced species replacement, while in others it may be less prominent or even non-existent. Therefore, future studies could benefit from a more localized spatial analysis to complement the broader trends identified in this study.

Our data spans two distinct time periods (2006-2009 and 2016-2018), which could be interpreted as a case of snapshot-resampling (Stuble et al. 2021). It has been proven that linear models are effective for analyzing this type of data under specific conditions. These conditions include scenarios where the richness of the assemblage is relatively high (around 50 species), when more than one year is resampled at the end of the study period, and most importantly, when the inter-annual variance is low (Brown et al. 2011, Stuble et al. 2021). Our case study meets all these requirements, indicating that the trends we estimated are quite robust.

While the temporal functional dissimilarity indices used in this study are useful to tackle our objectives, they are not without limitations. Functional richness (FRic, Villéger et al. 2008) is known to be dependent on taxonomic richness. This could potentially result in a methodological, rather than ecological, positive relationship between taxonomic and functional changes (Schleuter et al. 2010). This dependency seems to occur when precise numerical coding of functional traits introduces new functional entities with each species addition (i.e., any species added to or subtracted from the assemblage would produce a functional change), thus decreasing the index's ability to represent redundancy within the assemblage. However, our analysis highlights that out of 53 species only 14 are functionally distinct, indicating a significant level of functional redundancy within the community. Some of these functionally redundant species are vertices in the functional space, which could lead to an overestimation of functional change trends. Additionally, FRic does not take into account species with intermediate positions within the functional space that may be functionally unique (Legras et al. 2020). However, in our study, most species with high distinctiveness are also vertices in the functional space. This shows that these indices are effective in identifying functionally novel species. These findings confirm that the patterns we observed truly reflect ecological variations.

5. Conclusion

For the first time, we assessed changes in taxonomic and functional temporal β diversity of a demersal community of Patagonia using data independent from the fisheries. Our results show that the demersal assemblage of the SMG has undergone a compositional change in recent years (2006-2018) due mainly to an increase in species replacement, which resulted in an increase of functional replacement, without a net change in species or functional richness. In addition, the partitioning of taxonomic and functional dissimilarity revealed that taxonomic and functional nestedness and turnover contributed differently to overall β diversity. Our results suggest that both species and functional richness are being regulated at the local scale within the gulf.

We also found that the rise in occupancy of three species of crustaceans has a direct impact on the local assemblage's functional structure. Since species contribute differently to ecosystem functioning, a focus on species-level change can improve our understanding of temporal dynamics in marine assemblages. It must be noted that identifying the drivers of community change in marine assemblages is difficult, and different factors could interact with each other,

making it challenging to determine the cause of the observed patterns. Future studies should focus on temporal and spatial changes in anthropogenic (e.g., fishing effort) and oceanographic factors, which could provide the information required to better understand why species are being replaced in demersal communities of temperate ecosystems.

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Authors' contributions

JCN: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; MAR: investigation, methodology, writing—review and editing, project administration, funding acquisition, fishing surveys planning and execution; MOR: investigation, methodology, writing—review, project administration, fishing surveys planning and execution, funding acquisition; RG: investigation, methodology, supervision, writing—review, project administration, funding acquisition, fishing surveys planning and execution; AM: conceptualization, supervision, writing—review and editing; GMS: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing, fishing surveys planning and execution, project administration, funding acquisition.

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Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Species turnover drives functional turnover with balanced functional richness in a Patagonian demersal assemblage.

Josefina Cuesta Núñez, María Alejandra Romero, Matías Ocampo Reinaldo, Raúl González, Anne Magurran and Guillermo Martín Svendsen.

Highlights

- We estimated a rate of 15% of species replaced per decade in a Patagonian demersal assemblage subjected to intense fishing activity.
- The species turnover drives a functional turnover of 13% per decade.
- Increased occupancy of three crustacean species led to significant functional change within the community.
- Taxonomic and functional richness remained constant through the study period, indicating a community-level regulation of both variables.

Key words: β diversity, functional traits, global change, marine fish, marine crustaceans, trawl fishing**.**